COHERENCE BETWEEN THE SYMPATHETIC DRIVES TO RELAXED AND CONTRACTING MUSCLES OF DIFFERENT LIMBS OF HUMAN SUBJECTS

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SUMMARY

1. This study was undertaken to quantify the simultaneous sympathetic drives to muscles in the two legs of human subjects, and to elucidate the extent to which a common drive determines sympathetic outflow to different limbs at rest, during apnoea and during voluntary contractions.

2. Sympathetic efferent activity was recorded simultaneously from fascicles of both peroneal nerves, innervating the pretibial flexor muscles. At rest the similarity was quantified for a sample of records by manual measurement of equivalent bursts in the two recordings, and for all records by cross-correlation and power spectral analysis of the two recordings. During contractions, only the latter method was used.

3. At rest the correlation coefficient for the relationship between the burst amplitudes for the two recordings was 0·72 (S.D. 0·1). For the same sequences, the computed coherence between the two recordings was 85·6% (S.D. 6·7%) at the cardiac period. There was a statistically significant linear relationship between these two measures of similarity, and this was stronger when data from sequences recorded during apnoea were included in the analysis. At rest the mean difference in coherence between consecutive sequences with no intervening manoeuvre (apnoea, contraction, change in recording site) was 4·2% (S.D. 4·3%). In only two of forty-nine such instances was the difference in coherence > 10%.

4. Apnoea at end-expiration increased the amplitude and frequency of sympathetic bursts and increased the similarity between the two recordings. The correlation coefficients increased from a mean of 0·72 at rest to 0·89 during apnoea. Coherence increased from a mean of 82·1% at rest to 91·9% during apnoea.

5. On the right side, graded voluntary contractions were performed at 5, 10, 20 or 30% maximal force using the muscle innervated by the fascicle from which the recording was made. The coherence between the recordings made from the right and left legs decreased by > 10% at each contraction level. Pooling the data for all contractions, there was a significant decrease in power at the cardiac frequency in the

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sympathetic recording from the contracting leg. Contraction of a synergist or antagonist at 10% maximum produced negligible changes in coherence.

6. It is concluded that, at rest, homologous muscles of the lower limbs are subject to a common drive and that, during apnoea, this common drive can dominate the sympathetic outflow to the virtual exclusion of regional drives. During voluntary activity, the importance of this common drive is lessened, presumably because of regionally specific changes involving the contracting muscle. The data suggest that, at these relatively weak contraction levels, voluntary contraction leads to a reduction in sympathetic outflow to the contracting muscle.

INTRODUCTION

At rest, there is a remarkable similarity between sympathetic outflows to muscles in different limbs (Sundlöf & Wallin, 1977) and the extent of the similarity suggests that muscle sympathetic activity (MSA) is dominated by a common central drive. Differences between sympathetic drives to arm and leg muscles have been demonstrated during mental arithmetic (Anderson, Wallin & Mark, 1987) and post-contraction muscle ischaemia (Wallin, Victor & Mark, 1989). During the isometric contraction preceding muscle ischaemia there was no difference between sympathetic outflows to resting muscles in the opposite arm and the leg (Wallin *et al.* 1989), but no such recordings have been made from nerves innervating contracting muscles. However, there is indirect evidence that, at least under some conditions, there may be increased MSA directed to exercising muscle. Strong dynamic contractions of thigh muscles to 50–100% of maximum result in increased noradrenaline spillover to blood from the working muscle (e.g. Savard, Strange, Kiens, Richter, Christensen & Saltin, 1987), suggesting an increase in sympathetically mediated vasoconstrictor tone. Similarly, studies in intact rats and following acute sympathectomy suggest that, during locomotion, hindlimb blood flow and the flow to individual exercising muscles are under active sympathetic control (Peterson, Armstrong & Laughlin, 1988).

The present study was undertaken to quantify the degree of homogeneity in MSA direct to muscles of both legs at rest, during apnoea and during isometric voluntary contractions of muscles in one leg. By using the non-contracting leg as a control it was possible to separate regionally specific changes in MSA from generalized changes.

METHODS

Thirteen experiments were performed on twelve normal volunteers (seven male, five female, aged 20–34 years) with their informed consent and with the approval of the local ethics committee. Successful bilateral recordings of sympathetic activity were obtained in ten experiments; no data came from the other three experiments.

The subjects lay supine on a comfortable bed, with the upper body supported by pillows, the left leg unrestrained and the right leg secured in an isometric myograph. At the start of each experiment maximal dorsiflexion and plantar flexion forces were measured, and the subject was trained to contract tibialis anterior, extensor digitorum longus or triceps surae on the right side. The electromyogram (EMG) of appropriate muscles bilaterally and the electrocardiogram (ECG) were recorded using surface electrodes.

Neural recordings. Recordings of MSA were made bilaterally using tungsten microelectrodes introduced manually through the skin into the right and left peroneal nerves at the fibular head level. Details of the technique and evidence for the sympathetic nature of the activity have been

described elsewhere (Sundlöf & Wallin, 1977; Vallbo, Hagbarth, Torebjörk & Wallin, 1979). Fascicles innervating tibialis anterior were sought using the response to electrical stimuli delivered through the microelectrode as a guide. In nine of ten experiments, the fascicle from which MSA was recorded on the right side innervated tibialis anterior; in the tenth, the innervated muscle was extensor digitorum longus. When the tip of the electrode had penetrated the desired fascicle, its location was adjusted carefully under auditory control to bring the pulse-synchronous bursts of MSA into focus. On request subjects remained completely relaxed, held their breath at end-expiration ('apnoea') or maintained a contraction of the nominated muscle in the right leg for up to 6 min at a specified target force (5, 10, 20 or 30% of maximal voluntary contraction, MVC). All experimental data were stored on tape for subsequent analysis.

Sympathetic activity was amplified ($\times$ 10000–20000), filtered (bandpass 300 Hz–3 kHz) and stored on tape. On replay, it was refiltered prior to integration using a RC low-pass filter (time constant 0·1 s). This produced an analog signal that could be displayed on an ink-jet recorder or an electrostatic printer, or digitized on an IBM-compatible PC. Sequences were rejected when contaminated by the electromyogram of nearby contracting muscles.

Manual quantification. For seven subjects, data from four randomly selected 2 min sequences when the subject was at rest and one when apnoeic were replayed on an ink-jet recorder, with amplification adjusted such that the sizes of corresponding bursts in the two recordings were similar. The amplitudes of each burst of sympathetic activity in the two recordings were measured for the five sequences for the seven subjects, expressing each burst as a percentage of the largest burst in that sequence. The amplitude of a burst in the right peroneal recording was then plotted against the amplitude of the corresponding burst in the left peroneal recording for each sequence. Regression analysis was performed on these data, and the correlation coefficient taken as an index of the degree of homology of the two recordings (see Wallin *et al.* 1989).

Computer analysis. The integrated neurograms of the right and left peroneal nerve sympathetic activity were digitized in sequences of 2 min duration using a sampling rate of 0·1 kHz. Auto- and cross-correlograms were derived from the digitized data, and power-spectral analysis then performed on these correlograms (see Fig. 2). The cardiac period was identified from the ECG recording and confirmed in the auto-correlograms. The power in each recording was measured at the cardiac period. From the cross-correlated data the coherence between the two recordings and the gain of the relationship between the two were measured at the cardiac period (assuming that the left side was the input to and the right the output from the cross-correlogram).

Gain was computed as cross-spectral power divided by the input (left side) spectral power. Coherence was calculated as the square of the cross-spectral power divided by the product of the input and output powers. Because these measurements were made at the cardiac period, only noise at the cardiac period could have affected the measurements. This assumption was confirmed in control studies in which a neurogram was correlated with itself after noise was added to one input. The added noise was bandpass-filtered white noise (300 Hz–3 kHz). In different control runs this added signal was held constant, varied randomly or varied in time with the ECG. Only the latter decreased the coherence between the two signals by > 5%. This finding implies that increases in non-sympathetic neural traffic during a contraction (or undetected contamination of the neural recording by EMG activity would affect the measurements only if they possessed a cardiac periodicity. Although some non-sympathetic neural activity does have a cardiac periodicity (McKeon & Burke, 1981), such contamination would increase the power in the relevant recording: in the studies reported here, contraction was associated with a decrease in power at the cardiac frequency. In similar controls, changing the amplification of one input, slowly or abruptly, produced changes in coherence of < 5% provided that the gain change was not locked to the cardiac period. This finding implies that coherence would change minimally with minor disturbances to electrode position, were this to occur on the right side during contraction sequences. Such changes would, however; appear as a change in gain between the two recordings, much as is shown in Fig. 3.

RESULTS

Satisfactory bilateral recordings of sympathetic efferent activity to pretibial muscles were obtained in ten experiments on nine subjects. In all recordings there was, at rest, a striking similarity in the pattern and amplitude of the pulse-synchronous bursts of sympathetic activity destined for the muscles of opposite legs
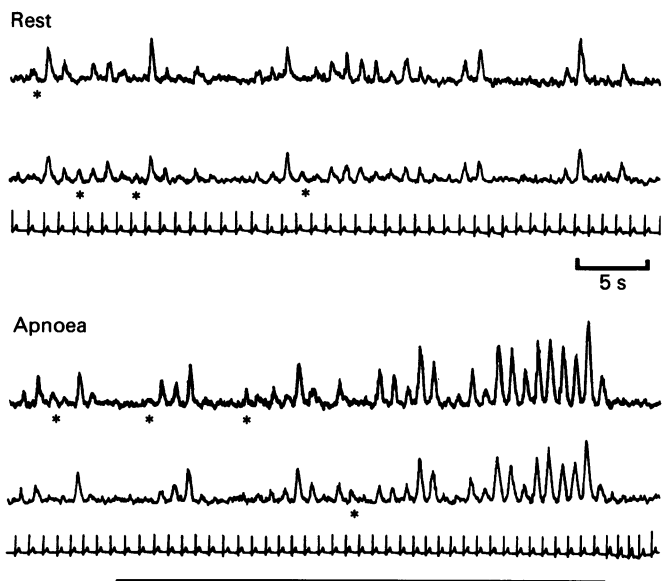
Rest

5 s

Apnoea

Fig. 1. Bilateral recordings of muscle nerve sympathetic activity from the right and left peroneal nerves showing the similarity of the integrated neurograms. In each panel the upper trace is the neurogram from the right leg, the second trace the neurogram from the left leg, and the third trace ECG. Bursts which appear only on one side are indicated by asterisks. In the lower panel, the subject was apnoeic for the duration indicated by the horizontal bar.
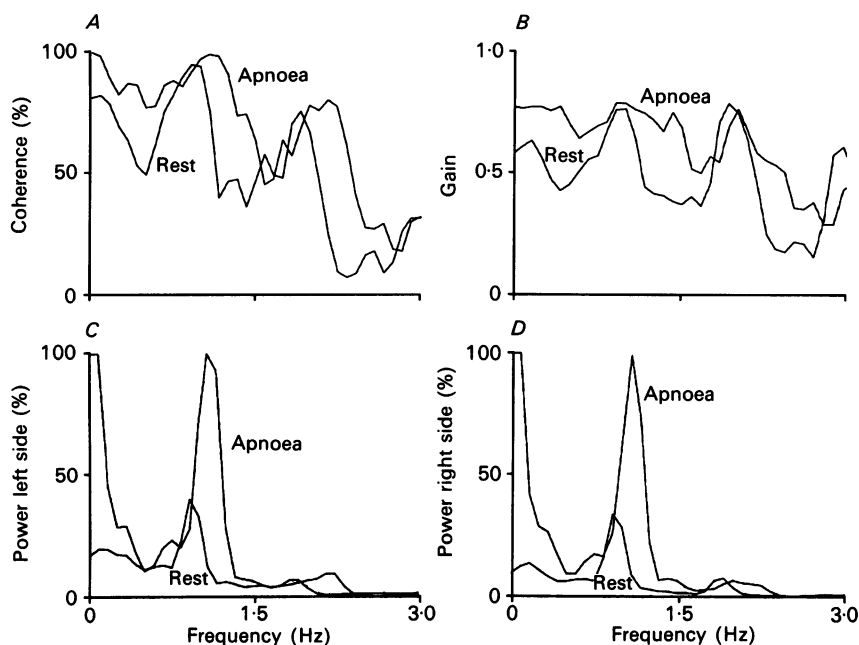

Fig. 2. Computer analysis of 2 min recordings, samples of which are illustrated in Fig. 1. Apnoea resulted in a marked increase in power bilaterally but only slight changes in gain and coherence. During apnoea the heart rate increased from 0·92 to 1·02 Hz.

(Fig. 1, upper panel). There were, however, small bursts that could be identified only on one side (indicated by asterisks in Fig. 1), and often the amplitude of a single burst did not have the same relationship to those of other bursts in the corresponding sequence on the other side. For the subject illustrated in Fig. 1, the correlation
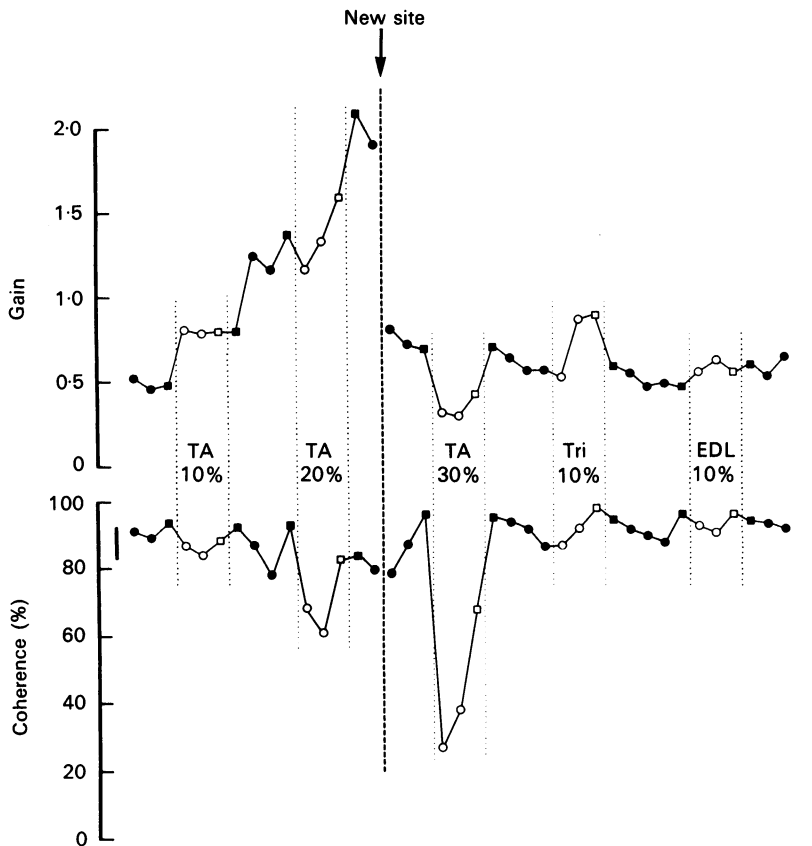

Fig. 3. The effect of different manoeuvres on coherence and gain plotted sequentially throughout an experiment. ● represent values obtained at rest, ■ represent values obtained when apnoea was performed by an otherwise resting subject, ○ represent values obtained during contraction, and □ represent values obtained when the subject was apnoeic during the contraction. The resting values for coherence changed little during the experiment, as indicated by the error bars on either side of the plot (± 1 S.D.). Coherence changed little with contractions of right tibialis anterior (TA), right triceps surae (Tri) or right extensor digitorum longus (EDL) at 10%. There were significant decreases in coherence with contractions of right TA at 20 and 30% MVC. In the initial part of the experiment there is a steady increase in gain, due to progressive dislodgement of the microelectrode on the left side. Despite this, coherence values at rest remained quite reproducible. At the dotted line the experiment was interrupted until a stable recording was obtained bilaterally.

coefficient between corresponding bursts on the two sides was 0·83 at rest and 0·92 during apnoea. Figure 2 illustrates the power spectral analyses for these two recordings. The computed coherences for these two recordings were 92·4 and 96·4%, at the cardiac frequencies 0·92 Hz and 1·02 Hz, respectively.

Homogeneity of the sympathetic drive to muscles of different limbs at rest

In each experiment the coherence between the two recordings was computed for the subject at rest, over five to fifteen 2 min sequences (average 10·2 sequences/experiment). The degree of coherence between the two recordings varied
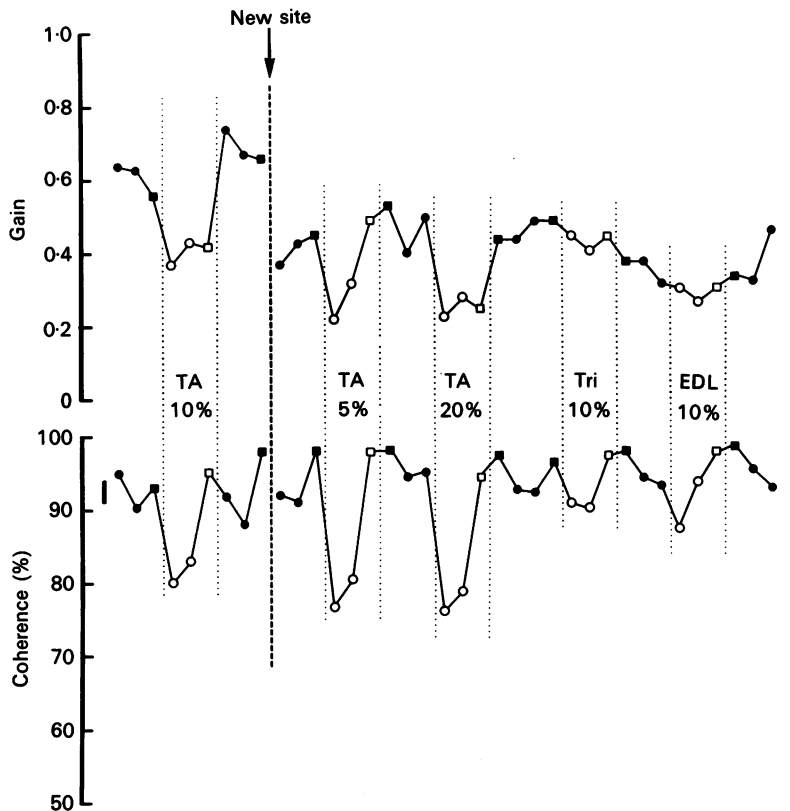

Fig. 4. The evolution of coherence and gain values throughout an experiment in a second subject. The symbols are as in Fig. 3. The reproducibility of the coherence when at rest is indicated by the error bars on either side of the coherence plot (± 1 S.D.). Coherence and gain decreased in the three contractions of right TA but changed little in the contractions of right triceps surae and EDL. The recording site on the right side was lost abruptly at the vertical arrow, so that the subsequent recordings had a different gain. However, the coherence values at rest were quite reproducible.

throughout an experiment. Some of this variability appeared to be related to a preceding manoeuvre, particularly apnoea, following which return to a truly basal state took several minutes (Figs 3 and 4). In the ten experiments the average coherence of all sequences at rest was 65·4–92·2 % (mean 82·1 %, S.D. 7·9 %). In some subjects the coherence values for all rest sequences in the experiment had S.D.s of 2–4 % despite many manoeuvres. The experiments with the highest variability had S.D.s of 9·5 and 12·8 %, respectively.

The difference in coherence between consecutive rest sequences with no intervening apnoea, contraction or change in recording site was determined to quantify the reproducibility of coherence measurements in the absence of these manoeuvres. The mean difference in coherence in forty-nine consecutive pairs of measurements was
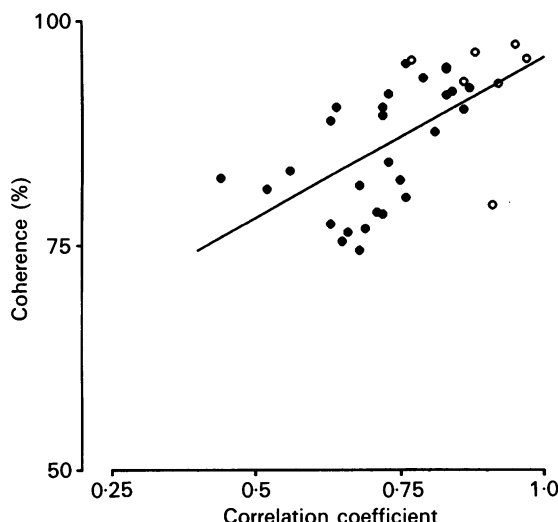

Fig. 5. Relationship between coherence and correlation coefficient for seven subjects. The values for sequences when the subject was at rest are indicated by ●. The values for the same subjects when apnoeic are shown by ○. The line represents the regression line for all data ($r = 0.60$, $P < 0.01$).

4·2% (S.D. 4·3%). In nine of the ten experiments, the mean differences were 0·1–6·5%; in the tenth experiment, one of only three values was 25·2%. Of the forty-nine consecutive differences, all but two were < 10%.

For seven subjects, the amplitudes of corresponding bursts were measured manually for four sequences at rest, and linear regression was performed on these measurements to provide correlation coefficients as a measure of the similarity of the activity on the two sides. The mean correlation coefficient of the four rest sequences for the seven subjects was 0·72 (S.D. 0·10) indicating that, in these sequences, 52% of the variance in the two recordings could be attributed to common drives. For these same twenty-eight sequences, the mean coherence was 85·6% (S.D. 6·7%). The sequences analysed for each subject were usually taken from different stages of the experiment. However, there were seven pairs of consecutive rest sequences, and the mean difference in correlation coefficient for consecutive sequences was 0·08. The mean difference in coherence for the same seven pairs of analyses was 5·7%.

When the data for the seven subjects were pooled, there was a significant linear relationship between coherence and correlation coefficient for the same sequences at rest (Fig. 5, ●; $r = 0.55$, $P < 0.01$). This relationship was improved when the larger bursts that occur during apnoea (see later) were included (Fig. 5, ○; $r = 0.60$, $P < 0.01$). Including the data obtained during apnoea did not alter the slope of the relationship. A positive correlation between coherence and correlation coefficient was

apparent in the five data points for six individual subjects, but there was no such trend in the data from the seventh subject. Excluding the data for this subject improved the correlation ($r = 0.71, P < 0.01$). It can be concluded that coherence and correlation coefficient represent valid measures of the homogeneity of sympathetic drive to different muscles, differing only in sensitivity.

TABLE 1. The effects of different manoeuvres on coherence

Manoeuvre	Coherence during manoeuvre	n	Control coherence	n
Apnoea	91.9 ± 2.13	9	82.1 ± 2.50	10
TA 5%	71.8 ± 7.91	3	90.4 ± 3.17	3
TA 10%	67.2 ± 5.80	8	83.7 ± 2.25	8
TA 20%	74.1 ± 3.20	4	85.9 ± 3.0	4
TA 30%	48.5 ± 7.40	3	84.5 ± 1.5	3
EDL 10%	88.9 ± 2.47	3	91.5 ± 1.39	3
Triceps surae 10%	86.3 ± 2.84	4	88.0 ± 2.88	4

Absolute coherence is expressed as a percentage, with mean ± S.E.M. n = number of subjects.

Effects of apnoea

In nine experiments, subjects held their breath in expiration ('apnoea') and, as illustrated in Figs 1 and 2, apnoea increased the size and frequency of sympathetic bursts in both recordings. This increased the coherence between the recordings (Figs 2A, 3 and 4). Power increased in both recordings to a similar extent (Fig. 2C and D) and consequently there were only small changes in gain (i.e. the common power in the two recordings divided by the power in the recording from the left leg), as shown in Figs 2B, 3 and 4.

Apnoea increased coherence in all but one experiment over the corresponding values at rest, the means being 82.1% (S.D. 7.9%) at rest and 91.9% (S.D. 6.4%) during the manoeuvre (Table 1). Different manoeuvres were not equally efficacious in the same subject, presumably because of variability in performance. The highest coherence values obtained during individual apnoeic sequences were 82.4–99.2% (mean 94.9%, S.D. 5.7%). These findings suggest that, under some circumstances, sympathetic activity with a cardiac periodicity may be determined almost exclusively by a central drive that is common to different body regions, to the virtual exclusion of regional differences.

The correlation coefficients for the relationship between the amplitudes of corresponding bursts in the two recordings increased during apnoea from 0.72 ± 0.10 at rest to 0.89 ± 0.07 during apnoea. For the same sequences coherence increased from 85.6 ± 6.7% at rest to 93.0 ± 6.2% during apnoea. As mentioned above inclusion of these seven data points in Fig. 5 improved the regression without altering the slope of the relationship.

Muscle sympathetic activity to contracting muscle

In eight experiments, steady isometric contractions were performed on the right side using the muscle innervated by the nerve fascicle from which MSA was being recorded (tibialis anterior, seven experiments; extensor digitorum longus, one

experiment). Simultaneous recordings of sympathetic activity were obtained from the left (control) leg and from the contracting right leg. The voluntary contractions increased the background neural noise generated by muscle afferents and non-sympathetic efferents in the nerve fascicle innervating the contracting muscle. This
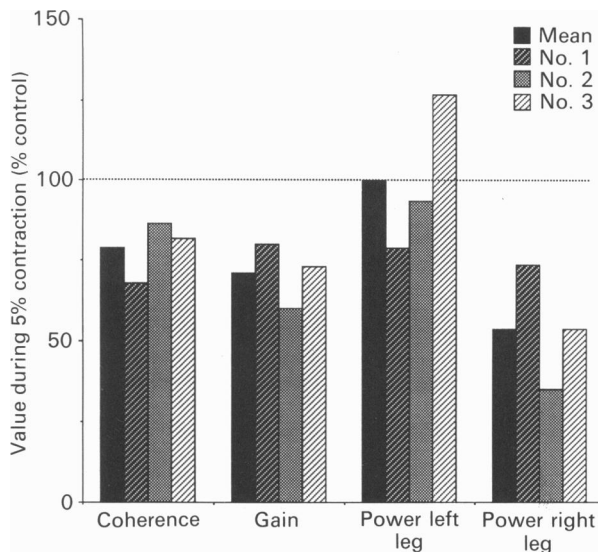

Fig. 6. The changes in coherence, gain and power for three subjects during contractions of right TA at 5% MVC. Data are normalized as percentages of the pre-contraction control values. For each data set, the filled bar represents the mean of the data for the three subjects. Coherence decreased in all three subjects, as did gain. The power in the recording from the contracting (right) leg decreased in all three subjects but, on average, there was no change in the power from the non-contracting (left) leg.

increase in noise invalidated manual measurements of burst amplitude from that side but did not alter the spectral analysis significantly because it did not contribute power at the cardiac frequency (see Methods). Furthermore, measurements of gain are dependent only on the cross-correlated (common) power in the recording from that leg.

Coherence decreased in all contractions, no matter what the contraction strength (Table 1). In five of six experiments in which contractions of different strength were tested, the stronger the contraction the greater was the decrease in coherence (Fig. 3A). However, this relationship disappeared in pooled data (see below), because different individuals were tested with different contraction levels and there was marked interindividual variability in the extent of the decrease.

With contractions of different strength (5, 10, 20 and 30% MVC), the average decrease in coherence exceeded 10% at each level (Figs 6–8). The decrease in coherence was accompanied by a decrease in power in the recording from the contracting leg at each contraction level. This change in power was not statistically significant at any of the levels, but when the data were pooled for all contraction levels in all subjects, it was statistically significant, whether the power during

contraction was compared with that in the preceding rest period (mean decrease 10·0 %; $P = 0·0079$; two-tailed paired t test) or with the mean of the power values for the preceding and subsequent rest periods (mean decrease 13·8 % $P = 0·0013$; two-tailed paired t test).
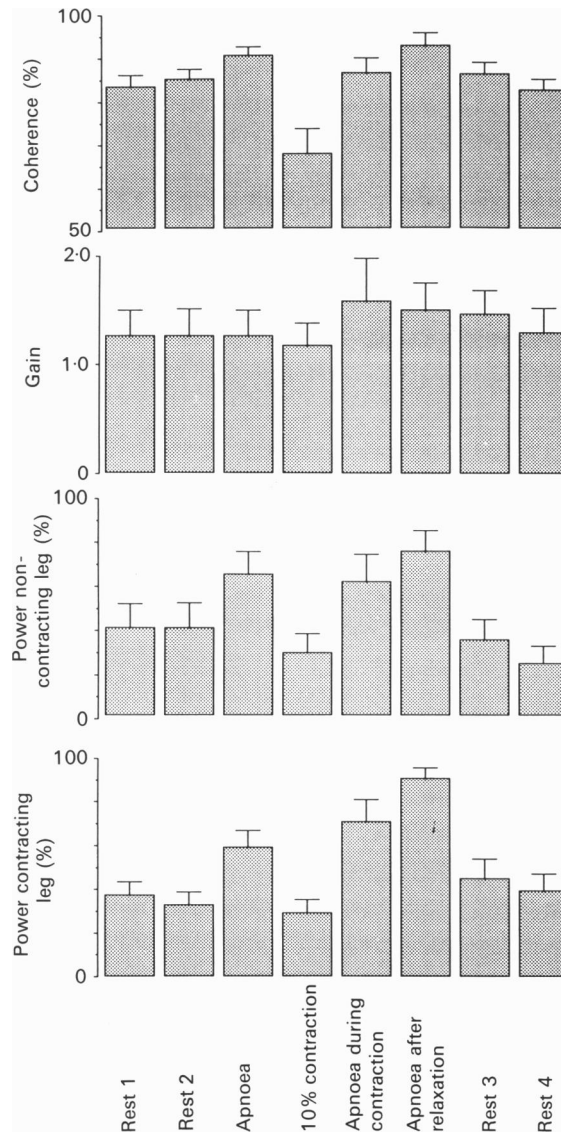

Fig. 7. Data for contractions of right TA at 10 % MVC. Each column represents the mean for eight subjects (± 1 S.E.M.).

There was no significant contraction-induced change in power for the non-contracting leg when the power value during the contraction was compared to that in the preceding rest period (mean decrease 5·7 %; $P = 0·2366$; two-tailed paired t

test). When compared to the mean of the power values for the preceding and following rest periods, there was a significant decrease in power, though to a lesser extent than on the contracting side (mean decrease 7·2%; $P = 0.0345$; two-tailed paired t test). As a result the gain between the two sides generally decreased (fifteen
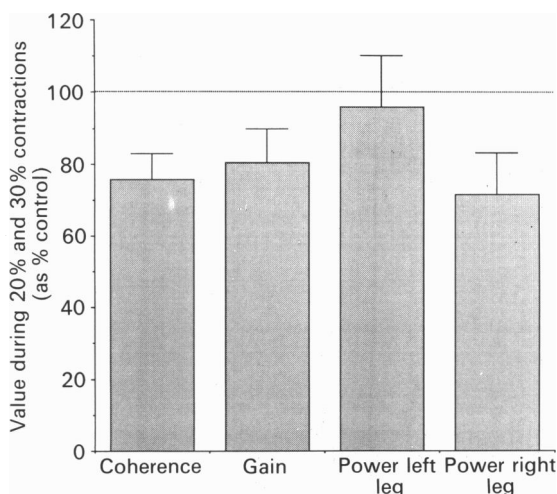

Fig. 8. Pooled data for contractions of right TA at 20 and 30% MVC, expressed as percentages of the pre-contraction control values ($n = 4$ at 20%; $n = 3$ at 30%). Each column represents the mean (± 1 s.e.m.). There are decreases in coherence, gain and the power for the contracting (right) leg, but no change in the power for the non-contracting (left) leg.

of eighteen trials). This change could be seen in the mean data for each contraction level, except at 10% MVC (Figs 6–8), and was significant when the data for all trials were pooled ($P = 0.0085$).

In determining the effects of contraction on power, the preferred comparison was with the power in the pre-contraction rest period rather than with the mean power in the pre- and post-contraction rest periods. The usual experimental protocol involved performance of apnoea at the end of a contraction and again immediately after relaxation, prior to the post-contraction rest period (see Figs 3 and 4). In some sequences, the increase in power due to apnoea subsided slowly, continuing into the post-contraction rest period. Similarly, apnoea prior to contraction (see Fig. 6) may have falsely elevated the mean power during the contraction in some sequences, but this would have minimized the contraction-induced change, not enhanced it.

Apnoea during contraction

Sustained apnoea during a contraction of the homonymous muscle restored coherence, often above the control values at rest but below values achieved with apnoea when not contracting (Figs 3, 4 and 7). The mean increases in coherence were 18·7, 16·5 and 15·7% with contraction levels of 10, 20 and 30% MVC respectively. However, when the apnoea was repeated on cessation of the contraction, coherence increased by a further 6·3, 3·3 and 19·3%, respectively. These changes occurred in all trials. During contraction, apnoea increased the power in recordings from both the

contracting and the non-contracting legs, generally in parallel (Fig. 7), but it increased the gain in ten of the fifteen trials due to a slightly greater effect on the contracting leg. As a result apnoea reduced the asymmetry in sympathetic outflow produced by contraction.

Contraction of other muscles

The effects of contracting a synergist (extensor digitorum longus, at 10% MVC; three experiments) or an antagonist (triceps surae, at 10% MVC; four experiments) were tested (Figs 3 and 4; Table 1). With contraction of the synergist, there was little change in coherence (on average a decrease of 2·6%), even though one subject found it difficult to prevent contraction of tibialis anterior when holding a steady contraction of extensor digitorum longus. With contractions of triceps surae, there was on average a decrease in coherence of 1·7%. With neither muscle were these changes significant; both changes fall well within the mean reproducibility of coherence measures for consecutive sequences (4·2%, see earlier). Apnoea when contracting a synergist or antagonist had similar effects as at rest.

DISCUSSION

The present results have quantified the similarity between the sympathetic efferent drives to homologous muscles in different limbs at rest, and demonstrated even greater similarity when subjects hold their breath in expiration. There is a significant decrease in this similarity when one of the homologous muscles contracts, and this is largely due to a decrease in sympathetic drive to the contracting muscle. Contraction of a synergist or antagonist at 10% maximal force has little effect on the symmetry of sympathetic outflow.

MSA has a prominent cardiac rhythmicity, and power, gain and coherence were therefore measured at the cardiac period. The analysis would not have measured all sympathetic activity because power at multiples of the cardiac period was ignored. However, the effects of this omission were small: the peak at the cardiac period dominated the power spectrum (see Fig. 2), and inspection of the plots indicated that the peaks at the cardiac period and at twice the period behaved in much the same way during contractions. During apnoea more heart beats were associated with sympathetic bursts than in the control situation, and this change may have accentuated the increase in power at the cardiac period.

Homogeneity of sympathetic drives

Total sympathetic outflow presumably depends on a balance between drives that are common to all muscle groups, and regionally specific drives of central or peripheral (reflex) origin. In subjects at rest there is probably no specific stimulus for regional variations in muscle blood flow and, accordingly, the coherence between sympathetic drives to muscles of different limbs was high in relaxed subjects. During apnoea the sympathetic outflow to muscle increases but again there is no reason why this drive should be distributed unevenly to the two legs.

Coherence decreased when one of the innervated muscles was contracted. This implies that the common drive had become less dominant and, by inference, that

regional drives were more important. However, this inference is valid only if a change in noise can be excluded as the cause for the decreased coherence. Inevitably contraction is associated with increased afferent and efferent traffic in the nerve fascicle innervating the contracting muscle, but this is unlikely to have affected the measurements for two reasons. First, an increase in noise would be expected to increase the power in the recording from the contracting leg, not decrease it as was consistently found. Secondly, the measurements of power, gain and coherence were made at the cardiac period because MSA occurs in pulse-synchronous bursts. Control studies indicate that only changes in noise that occur with a cardiac periodicity affect coherence (see Methods). Thus, regional factors, central or peripheral, assume greater importance in determining sympathetic outflow when subjects contract a muscle than when they are at rest.

In anaesthetized and decerebrate cats with all baroreceptors denervated, Kocsis, Gebber, Barman & Kenney (1990) determined the coherence between different sympathetic nerve pairs using a similar analysis to that used here. There was correlated activity in the 2–6 Hz range with different phase relationships that could be altered experimentally (e.g. by altering ventilation rate). These analyses indicate that the relationship between different sympathetic outflows is not immutable, a conclusion supported by the present findings. Their coherence values were generally lower than in the present study, some 50–70 %, and this raises the question whether the present analysis, restricted to power at the cardiac period, might have resulted in high coherence values that exaggerate the degree of similarity between the correlated recordings. In this context, it is notable that the correlation coefficient of the relationship between the amplitudes of equivalent sympathetic bursts suggests that, at rest, 52 % of the variance of MSA in the two recordings was due to a common drive, less than suggested by the coherence value. On the other hand, the baroreflex is responsible for the pulse-synchronous bursts seen in human MSA (Wallin & Fagius, 1988), and this would impose a high degree of similarity for nerves innervating muscle throughout the body.

Vasoconstrictor or vasodilator activity

There is strong evidence that the pulse-synchronous multiunit bursts of MSA are dominated by vasoconstrictor impulses which are influenced by arterial baroreflexes (Vallbo *et al.* 1979; Vissing, Scherrer & Victor, 1989). Vasodilator efferents are present in the skin of the human forearm and lower leg (Grant & Holling, 1938) and foot (Lundberg, Norgren, Ribbe, Rosén, Steen, Thörne & Wallin, 1989) and, although the question is not settled, some observations suggest that human muscle receives an active vasodilator innervation (Blair, Glover, Greenfield & Roddie, 1959). However, muscle vasodilator neurones in the cat are neither spontaneously active at rest nor influenced by arterial baroreceptors (Horeyseck, Jänig, Kirchner & Thämer, 1972, 1976). Thus, even if a putative vasodilator innervation of human muscle were important, the present analyses have probably avoided such activity by focusing on pulse-synchronous activity and activity in correlograms with a cardiac periodicity.

Changes in sympathetic activity associated with voluntary contraction

The findings of decreased coherence between the recordings from the two legs and decreased power in the recording from the contracting leg suggest that contraction of a lower limb muscle at 5–30 % MVC induced a local reduction of sympathetic, presumably vasoconstrictor, drive to that muscle. The specificity of this alteration is illustrated by the fact that no such change was found when the contraction involved not the innervated muscle but a neighbour in the same leg, be it a synergist or antagonist. A decrease in MSA would certainly add to metabolic factors tending to produce vasodilatation in the contracting muscle. Whether the underlying mechanism for the MSA reduction is a descending supraspinal influence or an inhibitory spinal reflex is unclear.

There has been no previous study of changes in MSA to contracting muscles, but one study of noradrenaline spillover led to the opposite conclusions (Savard *et al.* 1987). However, that study involved dynamic (rather than static) contractions of a large muscle mass performed at 50–100 % of maximal power for 10–20 min. Compared to our weak, fairly short-lasting contractions such efforts should be expected to produce a much greater cardiovascular load and therefore it would be reasonable to expect a difference in vasoregulatory neural outflow.

A number of studies have addressed changes in MSA to lower limb muscles during sustained contractions of muscles of the forearm or jaw (Delius, Hagbarth, Hongell & Wallin, 1972; Mark, Victor, Nerhed & Wallin, 1985; Seals, 1989; Elam, Johansson & Wallin, 1991). The common finding was an increase in MSA, particularly after contractions lasting more than 1 min. The degree of MSA increase is load and time dependent (Saito, Mano, Abe & Iwase, 1986; Seals & Enoka, 1989) and has been found to correlate to a decrease of intramuscular pH in the contracting muscles (Victor, Bertocci, Pryor & Nunnally, 1988). In contrast, recent studies suggest that static *leg* exercise does not increase MSA to the non-contracting leg (Ray, Rea, Clary & Mark, 1990, 1991). This finding is consistent with the present results.

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